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West-Eberhard and the notion of plasticity: Implications and consequences for an extended synthesis of evolution

Antonine Nicoglou

The biologist Mary Jane West-Eberhard publishes, in 2003, a book, entitled *Developmental Plasticity and Evolution*, in which a new synthetic approach, integrating development with evolution, is offered. For this reason, the book is seen as a piece of work in the field of Evolutionary developmental biology, commonly known as Evo Devo, whose aim is to synthesize data from both development and evolution. However, West-Eberhard's ambition is much higher in this book because she does not only focus on gathering the data from both fields, but she also wants to formalize a new synthetic theory of evolution, which includes development in its definition. She also explains that, in order to provide such a synthetic theory of evolution, she needs to offer an "inclusive definition of plasticity" in order to avoid "unnecessary distinctions at every turn" even if she assumes that such distinctions may be important for certain points. Our aim, in this article, is to explore the implications and consequences of West-Eberhard's "inclusive definition of plasticity" in such an attempt of a new synthesis of evolutionary theory, including development.

The origin of the problem

The book creates quite a stir in the biological community and among philosophers of biology with its publication and circulation (Pfenning 2004; Rollo 2004; De Jong 2005) because West-Eberhard's attempt is to propose a process for the emergence of evolutionary novelties that is no longer based on the single genetic mutations. In this new framework, genes are considered as "followers, not leaders in evolution". It means that the changes in genes frequencies are considered as following rather than initiating the appearance of adaptive traits. Such new process is the following one: a change in the environment of the individuals gives rise to a developmental plastic response and to a phenotypic accommodation - the immediate adjustment to the changes resulting from the multidimensional adaptive flexibility of the phenotype – which enables, as a second step, the improvement of the individuals' adaptation in the new environment. The new phenotypes, which result from this developmental plasticity, are then selected. Eventually, a change in allele frequency - the genetic accommodation - improves and integrates the change. In this new process, environment becomes a key participant in the generation and selection of adaptations. The first step of the process is thus "developmental plasticity".

Understanding what West-Eberhard exactly means by an "inclusive definition of plasticity" is a necessary preamble to a proper analysis of her view. The fact that she gives a central role to this notion of plasticity in her account and also that she provides an "inclusive definition", in order to encompass its different uses among the disciplines in biology, implies that she considers "plasticity", and more specifically "developmental plasticity" as an operative concept in a new synthesis of evolution, including development. This last expression means that the concept of plasticity, defined in a certain way, could be a central concept (Pigliucci & Müller 2010) in the realization of a strong theoretical synthesis of evolution, including development. However, several questions may be raised, and the main one would be: what does it mean for a concept to be central in the realization of a strong theoretical synthesis of evolution, including development? In order to answer this major question, two subsidiary questions are provided: (1) is it a concept that includes or synthetizes into the same definition different *uses* of the notion of plasticity, in different contexts and in different disciplines of biology; or (2) is it a concept that includes and synthetizes into the same definition different *meanings* that the term "plasticity" can adopt in the life sciences? By answering these questions I will show in which case one really gets a central concept, which helps thinking theoretically a new synthesis of evolution, that would include development.

To explain what I mean by the first subsidiary question, I will refer to the notion of "developmental plasticity". The notion has been frequently used in the past, particularly in neurobiology (Bennett et al. 1964; Baudry et al. 1993; Foehring & Lorenzon 1999). It refers to the changes in neural connections during development as a result of environmental interactions as well as neural changes induced by learning. The notion helps highlighting the specific change in neurons and synaptic connections as a consequence of developmental processes. It is one use of the notion, which is restricted to the field of neurobiology. But the notion of "developmental plasticity" has also been used in developmental biology (including genetic studies), about the developmental pathways for instance, where it accounts for the complexity of interactions between genotype and phenotype, during development, and based on environmental circumstances (Gilbert 2010). This second definition is different from the one in neurobiology, mainly because it refers to different entities. In both cases, the definition of "developmental plasticity" depends on the context and on the discipline concerned. Concerning the second subsidiary question, it is related less to the context of use of the notion but more specifically to the meaning of the term "plasticity" in biology. Indeed, the term can be understood in two different ways, two different meanings, which are based on the etymology of the term. In Greek, it can be linked to *plastikos*, which means, "related to the shaping" or "for the shaping", and to *plastikê*, from the verb *plassein*, which means "to mold" or "to form". Therefore, the term "plasticity" can either describe the ability the body possesses to model its form over time, as illustrated, for instance, by the limb growth studies in development (Forgacs & Newman 2005); or it can refer to alternative possible phenotypes as a result of environmental signals on a single genotype, as illustrated, for instance, with the differences of patterns on butterfly wings depending on the seasons in which they develop (Brakefield et al. 1996). Here the distinction does not depend on the context of study but on the particular point of view – from the "plastic result" or from the "plastic process" –, the biologist adopts.

In this paper, I will start by a brief epistemological analysis of the concept of plasticity in the life sciences in order to highlight the different "traditions of use" of the term in the field. In a second part, I will compare these traditions to West-Eberhard's concept of plasticity and examine, based on this comparison, what kind of an "inclusive definition" she offers. Eventually, I will suggest an answer to our major question, which concerns whether or not the concept used by West-Eberhard helps thinking theoretically a new synthesis of evolution, that would include development.

"Plasticity" in the life science: Two conceptual traditions of use

When speaking of "plasticity" in the life sciences, the first idea that comes to the mind of the contemporary biologist is the notion of "phenotypic plasticity". "Phenotypic plasticity" is commonly defined as "the property of a given genotype to produce different phenotypes in response to distinct environmental conditions". This definition, offered by Pigliucci (2001) and initially formulated by Bradshaw (1965), largely depends on the rediscovery of Mendel's law and the advances of genetics in the early 20th century. However, the term "plastic" (e.g. in an adjectival phrase) was also used long before the early days of genetics, particularly in embryology, to refer to the "architectonic" or "developmental properties" of the embryonic tissues. It was mainly this meaning of the word "plastic" that embryologists understood, when they used to refer to the term. Recently, developmental biologists have given a renewed attention to this use (e.g. in stem cells studies).

First, concerning the most common use of the term, the notion of "phenotypic plasticity", a conceptual definition has been provided in the "genetic tradition". The definition of Bradshaw of phenotypic plasticity, is the result of certain trends already well established in the young discipline of genetics. The definition of plasticity is both linked to the genotype/phenotype distinction (Johannsen 1911) and to the modified (after Woltereck 1909) concept of "norm of reaction", which is used to describe the reactions of the genotypic constituents in contact with various environments. When Dobzhansky (1955) introduces the notion to the Anglophone world, he focuses on the adaptive norm. For this reason, the origin of the adaptive norm becomes a basic problem of population genetics (Sarkar 1999). Since Bradshaw's definition of "phenotypic plasticity" is based on this concept of norm of reaction, plasticity also becomes a problem of population genetics. Because of the importance of genetics in the 20th century, "plasticity" becomes, for most biologists, a term of genetics (e.g., Bradshaw 1965; Schlichting 1986; Stearns et al. 1991; West-Eberhard 1989; Scheiner 1993; Sultan 2000). This tradition of use of plasticity is also linked to a certain meaning of the word, where the plasticity described is seen as the result of certain inputs. Most of the current definitions are based on this assumption.

Second, concerning the "embryological tradition" of use of the term "plastic", the focus on the notion has been given to emphasize the specificity of living beings compared to other elements of nature. Thus, Caspar Friedrich Wolff (1735-1794) (who is considered by some commentators as the "father" of descriptive embryology) thought that the matter in development is not a passive matter – such as preformationnist theories used to define it – but that its "plastic" characteristics have specific qualities, attributes and modes. At the earliest days of experimental embryology, and almost a century later, Hans Driesch (1867-1941) describes the egg during its division as a "harmonious equipotential system": each cell containing the latent potentiality (plasticity) to produce a complete organism. In 1928, Driesch managed to get a whole larva of urchin from a blastomere he had separated from a sea urchin embryo. With the development of cell biology, one of the great ambitions of embryologists (i.e., Johannes Holtfreter 1901-1992, Ross Harrison 1870-1959 and Viktor Hamburger 1900-2001) is the understanding of the cellular mechanisms responsible of morphogenesis – the developmental processes, which enable an organism to develop its form. The level of observation moves progressively from the body as a whole to the identification of tissues, group of cells and the molecular determinants, which appears to be decisive for the form development. The term "plasticity" is used to define entities property or processes property and not the result of the interaction of these entities with the environment. For instance, the term has been used a lot in stem cells studies, where it is assumed, by biologists, that these cells have "preserved plasticity" (Rinkevich & Matranga 2009).

Thus, there are two main traditions of use of the term "plasticity" in biology even if the second one is less represented in the literature than the first one. However, apart from this historical consideration, it seems, nowadays, that these two traditions have recently "merged" together or, rather, that the "genetic tradition" has supplanted the "embryological tradition". Indeed, from the early 20th century, the study of morphogenesis is located in an area where biologists, trained both in embryology and genetics, coexist (Morgan 1934; Waddington 1940). Yet, this area quickly disappears with the emergence and growth of new specialized fields in genetics, starting with population genetics, which enables biologists to achieve an explanatory synthesis in evolutionary theory between the data that it provides, along with mendelian genetics and the theory of natural selection, that will be called the Modern Synthesis. The study of development also takes a new turn with the emergence of molecular biology, where the study of the molecular determinants becomes central. Therefore, after this turn, morphology mainly focuses on these molecular determinants. This is the reason why embryological tradition will disappear and be replaced by a developmental tradition that gives a strong importance to molecular and genetic determinants. In her book, West-Eberhard seems to suggest that "development" also is overlooked with the emergence of molecular biology because it does not fit into the Modern Synthesis framework. For breaking the present stalemate, she suggests that the notion of "development has to be defined more broadly" than it used to be in embryology, in order "to include the ontogeny of all aspects of the phenotype, at all level of organization", and during the whole life cycle of the organism considered. This is another way, for West-Eberhard, to minimize the focus on genetic factors, but without reverting to the embryological tradition, which was focusing on the processes instead of the entities.

By doing so, West-Eberhard focuses on the phenotypes. Usually when talking about phenotype, biologists focus on morphological phenotype – the visible structures of the body that can be described – (e.g. size, shape, color…). In this context, "morphological plasticity" accounts for the possible morphological alternatives (i.e. polymorphism in the case of discrete alternative phenotypes, and norm of reaction in the case of continuous phenotypes). Thus, when it comes to phenotypic plasticity, "morphological plasticity" is the most common object of study for biologists (e.g. Greene 1989; Nijhout 1991; Van Buskirk & Steiner 2009). West-Eberhard extends the field of investigation of phenotypic plasticity, used in genetics, by referring to the concept of "developmental plasticity". This is partly what she intends to do in providing an "inclusive definition of plasticity". In order to understand precisely what kind of "inclusive definition of plasticity", West-Eberhard offers, I will now analyze, more precisely, her definition of plasticity and see if and, possibly, how it includes the different traditions described before?

West-Eberhard's inclusive concept of "developmental plasticity": Including what?

In her book, West-Eberhard seems to show that, in order to integrate development in evolutionary theory, one should no longer use the term "plasticity" in a very specific sense, but should use it in a much inclusive and a more general way, leaving aside the differences between the different meanings that the term can adopt, depending on the contexts and on the disciplines of use. She defines "plasticity" as "the ability of an organism to react to an internal or external environmental input with a change in form, state, movement or rate of activity." The definition does not focus on any level of the organism in particular, and thus it enables West-Eberhard to include, under the same label, different types of plasticity such as morphological, physiological, phenotypic, behavioural plasticity, but also, adaptive plasticity – which is linked to the genotype-phenotype map – and non-adaptive plasticity – which is independent from the genotype-phenotype map – and eventually possible and varied synonyms such as flexibility, malleability and deformability. Such an inclusive definition of plasticity is possible because she also defines development broadly. Other objects of study than those traditionally assigned to the field, are added. Where developmental biologists traditionally focus on "morphological phenotypes", West-Eberhard decides to add on their plate other types of "phenotypes". For instance, she considers that "structure phenotypes" do not only refer to morphological structures, but also correspond to "the organization of the phenotype at any level of analysis". Therefore, behaviors and physiological processes can also be considered as phenotypes. This attitude is prevalent among all behavioral ecology. However, if the definition of development West-Eberhard gives is broad, her definition of the "phenotype" itself remains relatively conventional since she refers to Johannsen's article from 1911. This definition implies that the phenotype is determined by the genotype and thus fits with the traditional genetic view. What can we conclude from this analysis of West-Eberhard's definition for our understanding of "developmental plasticity" as an operative concept in a new evolutionary synthesis that includes development?

In the beginning of this paper, I drew a distinction between two subsidiary cases for what an "inclusive definition" is, which helped to explain what would be, in my opinion, a full "operative concept in a new synthesis of evolution". In one case, it may mean that the concept is used to make a synthesis between its different uses in the different disciplines, and where there is no apparent distinction between the different meanings the term can adopt because it is a new operative definition that is provided. In another case, it may mean that the concept is used to make a synthesis between its different meanings in different fields of biology. In the second case, the "synthesis" realized is more like a synoptic view, where the different meanings of the term, used sometimes in the same discipline, remain distinct and both important into the "inclusive definition" of the concept.

But before coming back to this second case, regarding the first case and the question of a possible synthesis between the different uses of plasticity in the different disciplines, Pigliucci, in *Phenotypic Plasticity: Beyond Nature and Nurture* (2001), pointed out that there are different definitions or, different "types" of plasticity. However, he suggested that it is possible to "reconcile" these definitions by observation and comparison of the described phenomena because, whether it concerns alternative choices of a morphological structure, of a behavior, or of a physiological response, in all three cases what is described, he said, corresponds to phenomena that allow organisms to change in response to environmental challenges. It implies that it is possible here to have an inclusive definition in the first sense because the phenomena described are quite the same or understood in the same way. Likewise and more recently, De Witt and Scheiner (2004) have also proposed an inclusive definition of "phenotypic plasticity" as the "environmentally sensitive production of alternative phenotypes by given genotypes." This definition seems to match with the first case where different uses of the term, in different disciplines, are merged into a single definition. But these authors have also set out to analyze and to describe precisely "phenotypic plasticity", for which the definition belongs to the genetic tradition that I described before. For this reason, it seems that, here, the inclusive definition is not a new one, but is focused on a specific meaning of the term (plasticity in the genetic tradition, understood as a result). We suggest that West-Eberhard's own inclusive definition is not significantly different from these types of inclusive definitions. The synthesis realized with the concept of plasticity in West-Eberhard's work is of the same kind as Pigliucci's and de Witt and Scheiner, since it is based on the merge of different uses of the concept in different disciplines into a single definition. What West-Eberhard, eventually, adds is essentially a broader definition of development, which, linked to the concept of plasticity, allows her to consider other phenotypes than those usually considered, but it is not much more.

Accordingly, one can respond positively to the first subsidiary question. "Plasticity", as West-Eberhard defines it, is used to make a synthesis between different uses of the term plasticity, in different disciplines and in different contexts. But the focus of the definition stays coherent to match with the definitions of plasticity in the genetic tradition. She says, "plasticity" is "the ability of an organism to react to an internal or external environmental input with a change in form [which corresponds to the "structure phenotype"], state [which corresponds to behavior or physiology], movement [which corresponds to behavior] or rate of activity [which corresponds to physiology]". Despite this observation, her "inclusive definition" does not provide a clear-cut answer as regards to the debate on whether or not the resulting concept of plasticity is consistent enough to be considered as an operative concept for a synthesis. Indeed, ultimately her definition, as much as De Witt and Scheiner's definition, is only a renewed definition of the one formulated by Bradshaw in the 1960's, thus, based on the "genetic tradition". In each case, it is just a matter of proportion of which use in a specific discipline is included in the general definition and in which way. For West-Eberhard an "inclusive definition of plasticity" implies nothing more than shifting the focus from genes to phenotypes, what seems, at worst, problematic – regarding Johannsen's definition of the phenotype, which relies on the genotype and not on the development – and, at best, insufficient to offer an operative concept that would help thinking theoretically a new synthesis of evolution, that fully includes development.

Therefore, some clues are offered, considering the second option, and one can respond negatively. "Plasticity", as defined by West-Eberhard, is not used to make a second kind of a synthesis, to offer a synoptic view in a single definition of the different meanings that the term can adopt in the life sciences. West-Eberhard do emphasize the developmental component of the process involved in plasticity and she values an emphasis on developmental plasticity in her conception of evolution in order to show how development produces an adapted phenotype, necessarily linked to evolutionary ecology. So far, studies have shown that developmental plasticity exists and might have a genetic basis but it appears that too little attention has been paid to the polysemy of the term "plasticity" itself. Recently, the cell biologist Stuart Newman and his colleagues (Newman et al. 2009) have defined "plasticity" as "the array of pattern forming mechanisms that operate during the development of complex organisms" (e.g. adhesion, lateral inhibition, cohesion…). This last definition of plasticity can be considered as being part of the "embryological tradition" of plasticity, especially because it is not focused on the entities but on the processes. In this conception, plasticity is seen as a process property and not as a result. Although West-Eberhard's definition of plasticity tends to be inclusive and to encompass different uses of the term in different fields, it does not succeed to include and to give weight to Newman's definition as much as to traditional definition of phenotypic plasticity. She does not succeed to give the same weight to the different meanings of the term in biology and so she leaves apart one of the main tradition of use of the term: the embryological one.

Conclusive remarks

If I come back to my main question, which was "in which case one really gets a concept that realizes a new theoretical synthesis of evolution, including development"? My main problem was to decide if "plasticity", as defined by West-Eberhard, could be considered as an operative concept in this sense. West-Eberhard's definition of plasticity is just one example among others. But it appears that in many cases too much attention has been paid to the contexts of use of the concept of plasticity and not enough to the different meanings the concept of plasticity can adopt, separately from its context, in all its semantic aspects. Incidentally, it also appears that the two meanings, identified here, refer to two traditions of uses of the term in the life sciences, what I have called the "genetic tradition" – where the most famous concept of "phenotypic plasticity" has been depicted – and the "embryological tradition" – where another meaning of plasticity, less investigated, but still currently quoted by cell biologists, is used. West-Eberhard gives a specific importance in her work and in her definition of plasticity to development but she gives such an importance to a certain "field of development", that evolutionary biology have, in a way, already encompassed. Therefore, she omits a major part of the developmental tradition, which includes embryological studies. If the aim of a synthesis is to give a synoptic view of evolution with development, what I believe, one should pay more attention to this overlooked part, that is, the embryological tradition.

The concept of "developmental plasticity", offered by West-Eberhard, attempts to synthesize the uses of the term in development and in evolution, and it is already a major step, that not so many authors have been doing when they refer to the concept. It shows that the concept of plasticity might be a central concept for a new theoretical synthesis of evolution, including development. However, in West-Eberhard definition, the "inclusive definition" misses partly its goal by focusing on a too recent view of development, leaving asides what the Modern Synthesis, in its time, already left aside, the embryological tradition. I suggest that a new synthesis of evolution, including development, should pay attention to the whole tradition in development and not only to this tradition in development, that starts with the molecular biology. It is only in this attempt that the concept of plasticity may, indeed, be considered as a central concept for a new evolutionary synthesis, which fully includes development.

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